

Recolonisation potential of zooplankton propagule banks in natural and agriculturally modified sections of a semiarid temporary stream (Doñana, Southwest Spain)

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Abstract The viable propagule banks of a temporary stream were studied from sections with different agricultural history. Hatching of zooplankton (copepods, rotifers and cladocerans) was recorded in the laboratory under controlled temperature and light conditions from an agriculturally modified area with average hydroperiods of about a week per year and two semi-natural reference areas with average hydroperiods of more than 3 weeks per year. We found significant differences in both taxon richness and abundance of zooplankton hatching between areas, which were lower in the agriculturally modified section, compared to the reference sections. Another factor likely to have influenced hatching in our experiment was conductivity, which differed between the two reference sections and might have affected hatching at high conductivities. For restoration purposes, hydrological reconnection of stream

segments is important to facilitate dispersal from the high diversity upstream segments to the depleted sites downstream.

Keywords Rotifers · Copepods · Cladocerans · Hatching experiment · Species diversity · Hatchling abundance · Hydroperiod

Introduction

Propagule banks in temporary wetlands are important sources of species diversity and facilitate the recolonisation of the watercolumn by many aquatic invertebrates after rehydration of the habitat (Wiggins et al., 1980; Gyllstrom & Hansson, 2004; Tronstad et al., 2005). Emergence patterns from propagule banks are potentially useful indicators of the ecological integrity of wetlands (Angeler & Garcia, 2005). Resident zooplankton species remain dormant in the sediment of ponds during the terrestrial period. They hatch from the sediment after rehydration of temporary ponds and can contribute a large fraction of colonists at the onset of the aquatic cycle (Jenkins & Boulton, 2003; Frisch & Threlkeld, 2005). Such benthic-pelagic coupling (or coupling of the benthic zone and the water column in wetlands) influences the structure and dynamics of the pelagic community and the ecological and evolutionary dynamics in aquatic habitats (reviewed in Brendonck & De Meester, 2003; Gyllstrom & Hansson, 2004). Resting stages frequent

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in propagule banks are produced by many zooplankton species including Rotifera, Cladocera and Copepoda (Gyllstrom & Hansson, 2004). Calanoid copepods, cladocerans and rotifers produce sexual resting eggs, while diapause in cyclopoid and harpacticoid copepods is usually expressed in one of the late copepodid stages (Santer, 1998, Gyllstrom & Hansson, 2004).

Wetlands are among the most degraded of all ecosystems as a consequence of human activity (Green et al., 2002). Approximately two-thirds of Europe's wetlands have been lost since the beginning of the last century (COM, 1995). Recently, the importance of wetlands, in particular small ponds and pools, for biodiversity conservation has been recognised and is attributed mainly to both their disproportional large contribution to regional diversity (Oertli et al., 2002; Williams et al., 2004) and to their ecological role in the context of metapopulations and metacommunities (De Meester et al., 2005).

Invertebrate propagule banks in temporary wetlands are often challenged with habitat alterations imposed by intensive farming practises. Agricultural development and cultivation of wetlands involves drainage of the land and, as a result can reduce or eliminate the period when surface water is present (Brock et al., 1999; Zedler, 2003). Hatching of zooplankton is impacted by such alterations, and is likely to be reduced in sediments that have not been flooded for several years (Boulton & Lloyd, 1992). The water regime can have differential, taxon-specific impacts, thus potentially modifying the invertebrate community (Nielsen et al., 2000). The duration of the hydroperiod is one of the most prominent factors affecting communities and species diversity in temporary wetlands (Serrano & Fahd, 2005; Frisch et al., 2006; Waterkeyn et al., 2008).

For this study, we compared the zooplankton propagule bank in three stream sections of a mediterranean temporary stream with different agricultural history. We aimed to assess possible impacts of land use on species diversity and size of the viable propagule bank by comparing zooplankton hatching from sediments of an agriculturally modified stream section and two semi-natural, reference sections of a temporary stream in the laboratory. We hypothesised that the viable propagule bank in the agriculturally modified area would be less diverse and smaller compared to reference sections of the same stream with a more natural flow regime.

Materials and methods

Study area

The Guadalquivir marshland (also known as Marismas del Guadalquivir) occupy over 100,000 ha and include large areas of natural, temporary marshes, ricefields, fish ponds and a variety of other aquatic systems (García-Novo & Marín, 2005; Serrano et al., 2006; Rendón et al., 2008). Large areas of interconnected temporary streams, lakes and ponds flood when rains fall in autumn and winter and dry out in the summer.

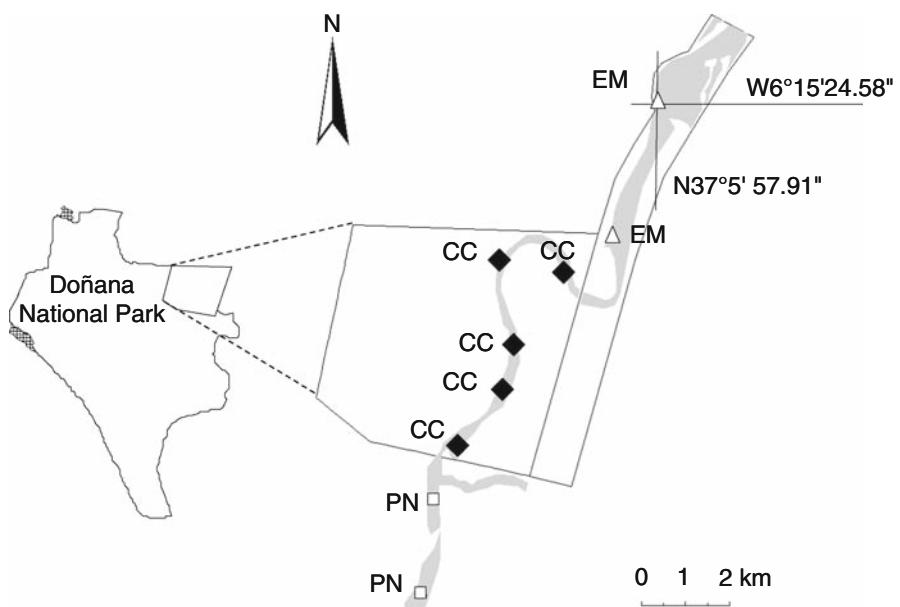
Sediment samples were collected from three areas within the Doñana wetlands: Entremuros (EM), Punta negra (PN) and the Caracoles channel (CC) (Fig. 1). All three segments are part of a temporary stream (the “Caño Travieso”), and became hydrologically disconnected from each other during the 1960s as a result of flood control measures. Two sections serve as reference zones (EM and PN) as they had no agricultural history and a semi-natural flood regime had been maintained.

Entremuros (EM) is a lower section of temporary stream that was canalised in the mid twentieth century to prevent flooding of surrounding agricultural fields during winter floods. EM was contaminated with waste from the Aznalcóllar mine spill in April 1998 (Taggart et al., 2006). The two sample locations of EM had an average hydroperiod of 2–3 weeks per year (estimated from teledetection data for the years 1994–2004 (Díaz-Delgado et al., 2006)).

Punta negra (PN) is part of the natural marshes protected within the core area of Doñana National Park declared a World Heritage Site in 1994. This area has never been transformed for agriculture and was not affected by the mine spill. PN is part of the “Caño Travieso” that, prior to transformation in the second half of the twentieth century, carried water southwards from the EM and CC areas towards the deepest part of the natural marshes. As for EM, the two sample locations in PN had an average hydroperiod of 3–4 weeks per year (estimated for the years 1994–2004 (Díaz-Delgado et al., 2006)). Soils are relatively saline here as water concentrates and evaporates in this area of lower terrain within the natural marshes at the end of the hydroperiod.

The Caracoles channel (CC) lies within the Caracoles estate (2,700 ha) that was originally

Fig. 1 Map of the study area. The stream is depicted in grey with three sections. Sediment was collected at two locations in Entremuros (EM, white triangles) to the northeast of Caracoles estate, at five locations within Caracoles estate (CC, black diamonds) and two locations in the Punta Negra section south of Caracoles estate (PN, white squares)



natural marshes transformed for agricultural use (mainly barley and other cereals) in the 1960s (Santamaría et al., 2005). At that time, the estate was isolated from surrounding marshes (including PN and EM) by constructing earth dykes along the west, south and east borders to prevent flooding. CC was originally the continuation of the Caño Travieso channel that brought water from the EM area down to PN and beyond during flooding events. In 2006, this connectivity was partially restored following the expropriation of the land and its incorporation into the National Park, removal of the dyke separating PN and CC, and the filling in of the drainage channels in the Caracoles estate (Santamaría et al., 2005). The removal of the eastern dyke separating CC from EM is scheduled for 2009. Due to effective drainage in Caracoles estate with a system of ditches and drainage pipes, water in CC was restricted to small rain pools with an average hydroperiod of less than 1 week per year (estimated for the years 1994–2004 (Díaz-Delgado et al., 2006)).

Sediment samples

Sediment samples were collected in 2004 during the dry season from three different sections of the Caño Travieso, at a time when all stream sections were dry. Sediment samples were collected from a total of nine locations (Fig. 1): five locations within the limits of

the Caracoles Estate (Caño Caracoles (CC), 29 July 04) and two locations in each of two reference sections (Punta Negra (PN) in Doñana National Park, and Entre Muros (EM), 18 November 04 (Fig. 1)). Three replicates were collected with a spade at each sample location (5×3 samples from CC, 2×3 from PN and 2×3 from EM). Replicates were taken from points separated by 2 m. Each sample had a size of 18×34 cm surface, and a depth of approximately 12 cm. Samples were transferred to individual plastic aquaria and stored dry in darkness at ambient temperature with a lid until the beginning of the experiment in February 2005.

The experiment was conducted in a plastic greenhouse between 8 February 2005 and 9 March 2005 under natural light and temperature conditions. The average water temperature in the aquaria was $19.4^{\circ}\text{C} \pm \text{SE } 0.29$. One replicate sample from CC was lost, reducing the total number of flooded samples to 26. Control aquaria ($n = 3$) without sediment were set up to monitor accidental introduction of propagules from external sources. On the first day of the experiment, all sediment replicates were flooded with well-water in individual plastic aquaria to a water depth of approximately 8 cm above the sediment. When adding the water, care was taken to avoid mixing of the original sediment layers. Zooplankton hatching was monitored in two of the three replicates of each location, on days 2, 4, 7, 10, 14, 17, 23 and 30. Water temperature and

conductivity were measured on each monitoring day before sampling (WTW Multi 340I multiprobe). The surface water was removed on each monitoring day by carefully pouring the water from the aquaria and controls. The water was then filtered through a nylon mesh ($64\ \mu$), the filtrate preserved in a final concentration of 6% formaldehyde and the filtered water reintroduced into the aquaria. The surface water in the third sediment replicate was not filtered until day 30 to allow for full development of hatching specimens in an undisturbed environment in order to obtain a more complete qualitative species list.

Faunal analysis

All hatchlings were counted at species level, except for bdelloid rotifers and neonate cladocerans. Counting was performed at $40\times$ magnification under a light microscope. For identification keys used for microcrustaceans see Frisch et al. (2006). Rotifers were identified following Koste (1978). For the quantification of cyclopoid copepods, we excluded all juvenile stages in order not to confound hatching juveniles and 1st generation offspring. Where adult cyclopoids could not be observed, but the presence of cyclopoid nauplii clearly indicated reproduction in the aquaria, we assumed the presence of one pair of adults on the previous monitoring day. In all cases the entire sample was quantified.

Statistics

Differences in conductivity between stream sections measured in the aquaria during the course of the experiment were analysed using repeated-measures ANOVA with monitoring days as repeated measurements and stream sections as the independent variable (CC, PN and EM).

For quantitative analysis of faunal data, all replicate samples from a given stream section for which hatching was quantified were included in the analysis. These were nine samples for section CC, and four samples for each of the reference sections EM and PN. Total taxon richness (cumulative number of all days) and monogonont rotifer species richness were analysed by ANOVA with stream section (CC, PN and EM) as the independent variable.

Total abundance of hatchlings (sum of all days) was analysed both with a univariate ANOVA and

with a MANOVA for the four main taxa (cyclopoid copepods, cladocerans, bdelloid rotifers and monogonont rotifers) as dependent variables and stream section as independent variable. Values for abundance were square-root transformed prior to statistical analysis to approach normality. Abundance of rotifers (bdelloid and monogonont) was included only for days 1–17 to account for the possibility of reproduction occurring in the aquaria in the longer time intervals (between days 17 and 23, and 23 and 30), and to avoid resultant inflation of numbers for the analysis. This was not necessary for cyclopoid copepods as only older copepodids and adults were quantified, nor for cladocera which did not reach the adult stage during the experiment.

Spearman rank order correlations were performed a posteriori between conductivity and taxon richness and between conductivity and total abundance for the reference sections EM and PN.

All analyses were carried out with STATISTICA 6, Statsoft Inc. (2001). (M)ANOVAs were followed by Tukey's HSD post hoc tests for unequal sample sizes available in the STATISTICA package and their *P*-values are given in the text to compare differences between stream sections.

Results

Daily measurements of conductivity ranged from 0.99 mS cm^{-1} in one of the CC samples to 32.7 mS cm^{-1} in one of the PN samples. It differed significantly between the three stream sections (repeated-measures ANOVA, $F_{2,23} = 30.52$, $P < 0.0001$). Conductivity was higher in aquaria containing sediment from PN than in those containing sediment from EM or CC (means 20.1 , 9.6 , 5.3 mS cm^{-1} , respectively $P < 0.001$). The difference in conductivity between CC and EM aquaria was not significant ($P = 0.156$).

A total of 15 zooplankton taxa were found to hatch from sediment samples from the three areas of the Caño Travieso temporary stream (Table 1), including Copepoda, Cladocera and the rotifer classes Bdelloidea and Monogononta. Cyclopoid copepods, bdelloid and monogonont rotifers hatched from all stream sections, while cladocerans were only found to hatch from EM (a total of two individuals of *Ceriodaphnia* sp.). Monogonont rotifers were the most diverse

Table 1 Number of individuals hatching during the 30-day experiment and information on species hatching from sediment samples

Taxon hatching	CC			PN			EM		
	Mean	SD	Qual.	Mean	SD	Qual.	Mean	SD	Qual.
Number of replicates	9		5	4		2	4		2
Copepoda									
<i>Metacyclops minutus</i> (Claus) 1863	5.8	4.3	✓	0.5	1.0	✓	0.5	1.0	✓
Cladocera									
<i>Ceriodaphnia</i> sp. juv. Dana, 1853	–	–	–	–	–	–	0.5	0.6	–
Rotifera									
Monogononta									
<i>Asplanchna</i> sp. Gosse 1850	–	–	–	–	–	–	0.5	1.0	–
<i>Brachionus</i> sp. Pallas 1766	0.2	0.4	✓	–	–	–	0.5	1.0	–
<i>B. angularis</i> Gosse, 1851	–	–	–	–	–	–	1.0	1.2	–
<i>B. plicatilis</i> Müller, 1786	0.1	0.3	✓	4.5	3.1	✓	30.0	34.9	
<i>B. quadridentatus</i> Hermann, 1783	–	–	–	0.3	0.5	–	0.3	0.5	–
<i>B. urceolaris</i> Müller, 1773	–	–	–	1.5	1.7	–	85.8	170.8	–
<i>Cephalodella gibba</i> (Ehrenberg, 1832)	–	–	–	–	–	–	49.0	96.0	–
<i>Gastropus hyptopus</i> (Ehrenberg, 1838)	1.9	3.0	–	2.8	4.2	–	474.0	494.3	–
<i>Hexarthra fennica</i> (Levander, 1892)	0.3	1.0	–	–	–	–	–	–	✓
<i>Lecane</i> sp. Nitzsch, 1827	–	–	–	–	–	–	0.3	0.5	–
<i>L. cf. candida</i> Harring & Myers, 1926	–	–	–	–	–	–	–	–	✓
<i>L. lunaris</i> (Ehrenberg, 1832)	–	–	–	–	–	–	–	–	✓
Bdelloidea Hudson 1884	123.8	237.3	✓	0.3	0.5	–	22.8	37.6	–
Total number of taxa		6		6			15		

Numbers are means per sample and stream section. Means are calculated from all quantitative samples of the three stream sections studied

–, No individuals observed; ✓, species present in qualitative sediment replicate treatment. Total number of taxa includes quantitative and qualitative samples

group (12 species), while Cladocera and Copepoda were only represented by one species each (*Ceriodaphnia* sp. and *Metacyclops minutus*, respectively). Figure 2A shows average taxon richness calculated from replicate sediment samples. For cyclopoid copepods, bdelloid rotifers and cladocerans (represented by one species each) the graph mainly reflects the prevalence of a given taxon in replicate samples, e.g. cyclopoid copepods were present in all replicate samples of CC and therefore had the value 1 in this area, whereas they were missing in some of the PN and EM samples, which show a value <1 for this taxon (Fig. 2A). Cumulative taxon richness for all three stream sections (Fig. 2B) approached saturation between days 25 and 30 of the experiment. The EM section had the highest taxon richness (15 taxa), while the number of taxa retrieved from CC and PN was six each. All monogonont rotifer species

recorded in CC and PN are a subset of those of EM, which contained all recorded rotifer species.

An ANOVA showed that taxon richness of the viable propagule bank of the three stream sections differed significantly (Table 2A). Richness was significantly higher in EM compared to CC (mean 5.8 ± 1.32 SE and 2.2 ± 0.36 SE, respectively, $P = 0.012$). PN had an intermediate taxon richness (mean 3.3 ± 0.95 SE), but differences with EM or CC were not significant ($P = 0.17$ and $P = 1.0$, respectively). As the only group represented by more than one species, monogonont rotifers showed significantly different species richness between stream sections (Table 2A) and were most diverse in EM. As with total taxon richness, this relation was only significant between EM and CC (means 4.3 ± 1.11 SE and 0.9 ± 1.05 SE, respectively, $P = 0.029$). Rotifer species richness in PN was intermediate

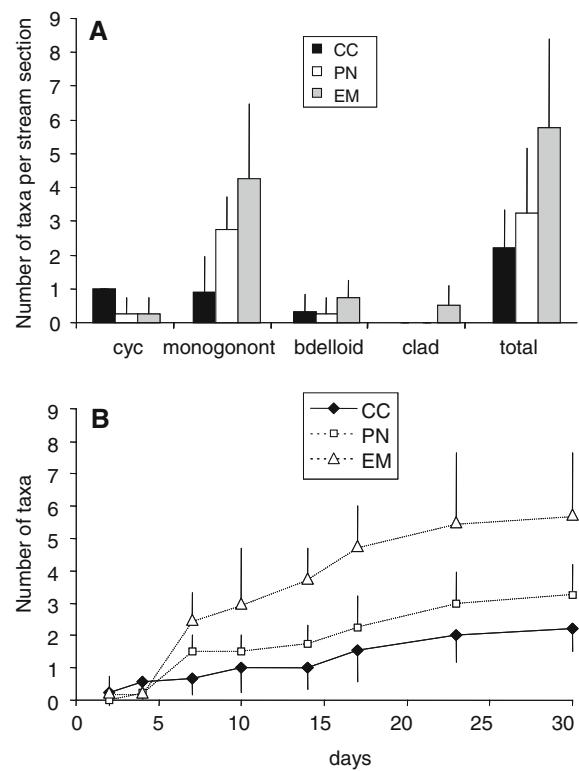


Fig. 2 **A** Average taxon richness for cyclopoid copepods (cyc.), monogonont and bdelloid rotifers and cladocerans (clad.). Monogonont rotifers were the only group for which more than one species was recorded. **B** Cumulative taxon richness as a sum for all taxa hatching from sediment samples of the three stream sections

(mean 2.8 ± 0.48 SE), but the difference with EM or CC was not significant ($P = 0.30$ and 0.17 , respectively).

Stream sections did not differ significantly in the abundance of hatching zooplankton measured as the

total of all taxa (Tables 1, 2B, ANOVA results). In contrast, taxon-specific abundance did differ between stream sections (MANOVA results in Table 2B, and Fig. 3), but with the exception of cyclopoid copepods these differences were only significant between EM and CC sediments. Cladocerans only hatched from EM and were significantly more abundant in samples from this area ($P = 0.047$). Monogonont rotifers were most abundant in EM compared to both CC and PN ($P < 0.007$). The most abundant rotifers in the EM samples were *Brachionus plicatilis*, *B. urceolaris*, *Cephalodella gibba* and *Gastropus hyptopus* (Table 1). In contrast, copepods (*Metacyclops minutus*) hatched in highest numbers from CC ($P < 0.015$). Although overall bdelloid rotifers were more abundant in CC than in the other stream sections (Fig. 3) this difference was not significant, due to large variation between replicates.

To test for correlations between taxon richness or hatching abundance and conductivity and to exclude the interaction with hydroperiod we performed Spearman rank correlation analyses between the two reference sections EM and PN which had a similar hydroperiod. While taxon richness was not significantly correlated with conductivity (Spearman $R = 0.46$, $P = 0.244$, $n = 8$), we found a significant negative correlation between conductivity and hatching abundance (-0.71 , $P = 0.047$, $n = 8$).

Discussion

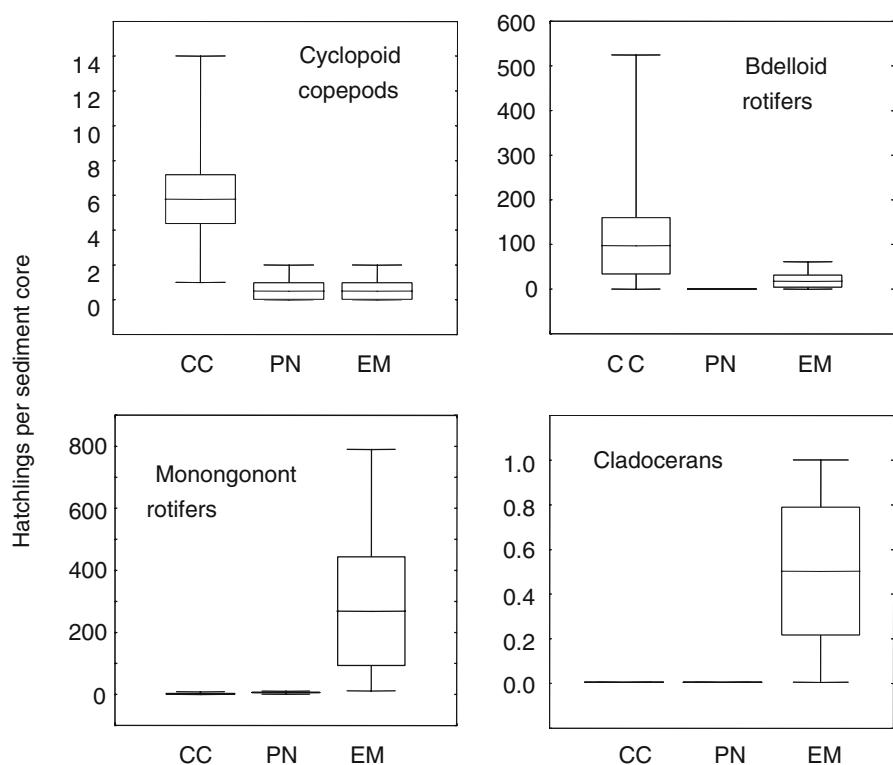
Our findings support our hypothesis that the viable propagule bank in the agriculturally modified area is less diverse and smaller compared to reference sections with a more natural flow regime. In the

Table 2 (A, B) Results of the (M)ANOVAs on zooplankton hatching from sediments of three sections of a temporary stream

	DF effect	DF error	F	P
<i>(A) Taxon richness of hatching zooplankton</i>				
Total taxon richness (ANOVA)	2	14	5.88	0.014
Monogonont rotifer species richness (ANOVA)	2	14	8.86	0.003
<i>(B) Abundance of hatching zooplankton</i>				
Total abundance (ANOVA)	2	14	4.31	0.075
Taxon-specific abundance (MANOVA, Wilks test)	8	22	4.14	0.004

Total taxon richness was measured in each replicate as the cumulative number of all zooplankton taxa recorded throughout the entire study period. Total abundance is the sum of all individuals that had hatched from the experimentally inundated sediments (see Methods for a more detailed explanation)

Fig. 3 Abundance of hatchlings in sediment samples of three stream sections of the Caño Travieso (boxes = SE, whiskers = min./max.). Note different scales for the y-axes for each taxon. Abundance of copepods and cladocerans include all days of the experiment, while for monogonont and bdelloid rotifers abundance only includes days 1–17 of the experiment



Mediterranean region, agricultural land use often causes major modifications to the hydrology of wetlands (Green et al., 1996, 2002), and this was the case in the Caracoles Estate. In both reference sections (EM and PN) a semi-natural flow regime had been maintained at the time of our study, whereas the CC section had been subject to intensive cultivation and drainage for the previous 20 years. Although the hydrological connections between the EM, CC and PN sections had been cut off during the previous two decades, short-lived rain-fed pools were present within the old streambed of CC during periods of heavy rain. These small pools had an average hydroperiod of less than a week per year. In contrast, hydroperiods in the reference sections EM and PN were 3–4 weeks per year (Diaz-Delgado et al., 2006). Hydroperiod appears to have been a major factor determining the size and diversity of the propagule bank in the Caño Travieso temporary stream. Both richness and taxon-specific abundance of zooplankton hatching from the agriculturally modified CC sections was much lower compared to the reference sections, especially EM. These results corroborate trends found in a previous hatching study (Gleason et al., 2004), who found that the eggbanks of restored wetlands had

significantly higher invertebrate taxon richness and abundance than drained wetlands. A study of aquatic invertebrates in temporary wetlands in the Camargue, France, concluded that species richness had a positive relationship with hydroperiod length, but a negative one with salinity (Waterkeyn et al., 2008).

Our study shows that not all taxa respond equally to the same stressors. In particular, we found *Metacyclops minutus* to emerge in significantly higher numbers from the propagule bank of the agriculturally modified stream section. This species is a successful colonist of highly ephemeral waterbodies with an exceptionally short life cycle of about a week (Maier, 1992; Frisch & Green, 2007). In previous studies in ponds of Doñana, it was found in the smallest, most short-lived ponds (Serrano & Fahd, 2005), and in salinities up to 28 mS cm⁻¹, or a combination of both (Frisch et al., 2006; Frisch & Green, 2007). Likewise, the higher abundance of bdelloid rather than monogonont rotifers in the CC sediments reflects the unstable and short-lived aquatic environment in this stream section. Bdelloid rotifers can respond quickly to desiccation by entering anhydrobiosis, a dormant stage triggered by desiccation and terminated by rehydration (Ricci &

Carprioli, 2005). In contrast, monogonont rotifers were significantly more abundant and diverse in the long hydroperiod, intermediate salinity section EM. This group is generally more frequent in habitats that become unsuitable cyclically since the production and hatching of resting eggs in monogonont rotifers requires more complex environmental cues (Ricci & Carprioli, 2005). Most likely, cladocerans were restricted to the same area for a similar reason.

Particularly in arid or semiarid zones, anthropogenic salinisation caused by irrigation and clearance of natural vegetation is a major stressor in wetlands (Williams, 1999). In our study area, the Caracoles estate had relatively saline soils prior to cultivation, and agriculture was heavily subsidised. Constant drainage of direct precipitation may even have lowered soil salinities in the area over time, and our sediment samples from the CC section showed the lowest salinities. Since conductivity did not differ significantly in the aquaria containing CC and EM sediments, the greater abundance and diversity of hatching zooplankton in EM is unlikely to be related to conductivity.

In contrast, conductivity in the PN aquaria was much higher, reaching levels likely to have negative impacts on diversity and abundance of emerging zooplankton (Nielsen et al., 2003) as well as on the active invertebrate community in the water column (Wollheim & Lovvorn, 1995; Green et al., 2005). Thus, high conductivity is likely to explain why PN showed lower hatching abundance than EM, despite similar hydroperiods. While hatching abundance was negatively correlated with conductivity in the two control sections, taxon diversity was not. Freshwater waterbodies with moderate salinity often have a diverse halotolerant fauna (Alonso, 1990), which is generally reflected in the zooplankton fauna of Doñana. It is possible that the high conductivity in the aquaria inhibited hatching from the PN sediments, while diversity was less strongly affected, but more detailed studies are needed to substantiate this.

Our results show that, even after decades of agriculture and near-elimination of flooding events, sediments in the bed of a temporary Mediterranean stream retain a zooplankton propagule bank that can aid recolonisation of aquatic communities upon hydrological restoration. However, the propagule bank of reference areas was significantly more diverse and abundant, supporting Angeler & Garcia's (2005)

suggestion that wetlands under continuous stress (e.g. caused by drainage) cannot recover from eggbanks alone. A successful restoration of zooplankton communities in temporary streams such as the Caracoles channel can be promoted by hydrological reconnection and interchange with semi-natural upstream sections. Such a reconnection is planned in our study area, and will facilitate the dispersal and recolonisation of zooplankton communities into areas further downstream. Additionally, the Doñana wetlands hold spectacular concentrations of waterbirds (Rendón et al., 2008), which are also important as vectors facilitating the recolonisation of restored wetlands in the area by invertebrates (Frisch et al., 2007).

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